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Discoid gemmae in *Radula*

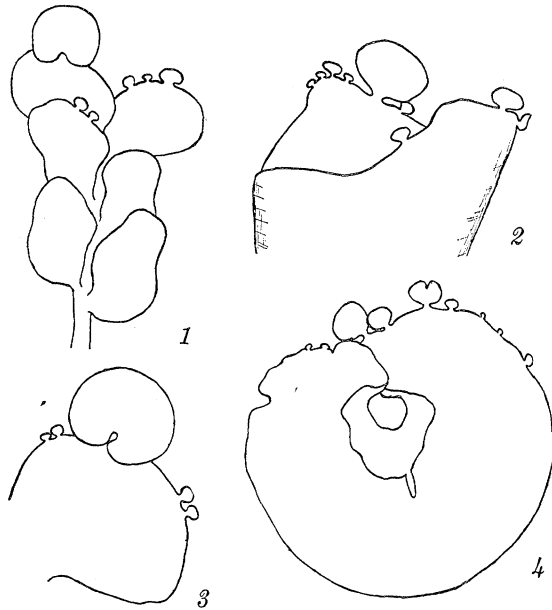
RUTH WILLISTON

Discoid gemmae, borne on the margins or surface of the leaves or on the thallus, have been reported in the following twelve genera of the Jungermanniales: *Metzgeria*, *Radula*, *Porella*, *Metzgeriopsis*, *Colurolejeunea*, *Diplasiolejeunea*, *Cololejeunea*, *Leptocolea*, *Aphanolejeunea*, *Lejeunea*, *Cyclolejeunea*, and *Frullania*. (See Evans, '04, '10, and '11.) It is probable, however, that they occur in others. In *Radula* they are definitely known in only seven species, although the genus, according to Stephani ('10), contains 220 species in all. In two species, *R. Hedingeri* and *R. tjibodensis*, the development of the gemmae has been carefully studied by Goebel ('87). A third species, *R. complanata*, was investigated by Cavers ('03) and later by Stevens ('10). In *R. flaccida* gemmae were observed by Gottsche ('63), in *R. Lindbergiana* by Jack ('81), in *R. protensa* by Schiffner ('93), and in *R. subtropica* by the writer; but no details about the gemmae in these four species have as yet been published. The present paper will be largely devoted to the gemmae of *R. flaccida* and *R. protensa*, although the other species will be included in the discussion.

RADULA FLACCIDA

This species was first described from Mexico in 1847 by Lindenberg and Gottsche (Syn. Hepat. 726). It has since been found widely distributed throughout the West Indies and the lowlands of tropical America. The material used in this study was collected by Dr. A. W. Evans at Bath, Jamaica (no. 332). *R. flaccida* is a dioecious species with a prostrate stem. It is epiphyllous. The gemmae are disklike bodies, one cell thick, attached to the dorsal margins of the leaves. They are the largest and most highly differentiated gemmae known in the genus, averaging at maturity 0.5 mm. in diameter, while the leaves themselves measure only 0.8 mm. in length. The cells nearest the center of the gemmae are the largest, averaging 0.02 mm. in diameter.

Toward the periphery they decrease gradually in size, those at the very edge averaging about 0.01 mm. Gemmae occur in this species on leaves of vegetative branches (FIG. 3), on male bracts (FIG. 1), on the margins of old perianths (FIG. 2), and on other gemmae (FIG. 4). Gemmae occurring on leaves or bracts were most numerous along the acroscopic margins, and in no case were gemmae found on the lobules of the leaves. There is apparently some relation between the stage of development of a vegetative branch and its capacity to produce gemmae, for the gemmae are rarely



FIGURES 1-4, *Radula flaccida*. 1, male bracts and proliferation of antheridial branch bearing gemmae, $\times 266$. 2, old perianth bearing gemmae, $\times 66$. 3, normal vegetative leaf with gemmae, $\times 266$. 4, small gemmae growing on the margin of a mature gemma, $\times 66$.

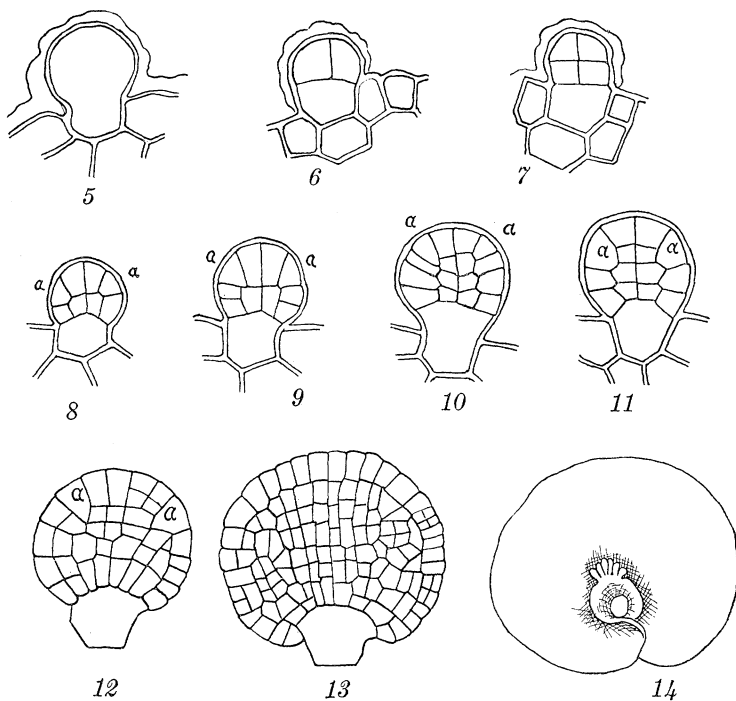
found on young plants. The fact that gemmae are never found on the youngest leaves indicates, however, that their production does not absolutely limit the growth of the shoot. When a branch produces gemmae at all, they generally occur on several of the leaves. A leaf may produce gemmae singly or in groups. In the latter case two or three gemmae are usually found together,

though groups of seven or eight may occur. In instances where more than one are produced on a single leaf, usually only one matures, and the others either become abortive or delay their development until the first one is shed.

In the development of the gemmae the sequence of cell division can be traced accurately only in the earlier stages, as with the increasing complexity of the gemmae the order of cell formation becomes somewhat variable. The formation of a gemma begins by the enlargement of a single marginal cell and its protrusion beyond its neighbors. This cell begins at once to secrete a transparent gelatinous substance. A similar secretion was noted in the early stages of *R. complanata* by Stevens ('10, p. 369), who suggests that the presence of this gelatinous substance may be taken as a rough indication of the region of most rapid growth. As this cell increases in size and pushes farther beyond the margin of the leaf, it takes on a knoblike shape (FIG. 5), and finally the end of the knob is cut off by a wall parallel to the margin of the leaf (FIG. 6). The inner of the two cells thus formed is the stalk cell, the outer the mother cell of the gemma. The stalk cell undergoes no division but increases slightly in size. The outer cell, however, soon divides by a median wall at right angles to the first. Each of the resulting cells then divides by a transverse wall. The original mother cell is now separated into quadrants (FIG. 7). The two outer quadrants are triangular in shape and generally begin at once to function as two-sided apical cells, cutting off segments first on the side toward the median line then on the side toward the lower quadrant, and so on until three or four segments have been formed (FIG. 8, 9, 10, 11, 12). The earlier segments divide first by periclinal walls and later by anticlinal walls, so that by the time the last segment is cut off by the apical cell the first may have divided into as many as six or eight cells. The apical cells both cease to function after a short time; and instead of cutting off segments in the normal way each divides by a periclinal wall followed by an anticlinal wall in the peripheral cell, thus giving rise to three cells.

The establishment of the apical cells is not always simultaneous on the two sides of a single gemma. The original triangular quadrant on one side or both may cut off an extra cell parallel

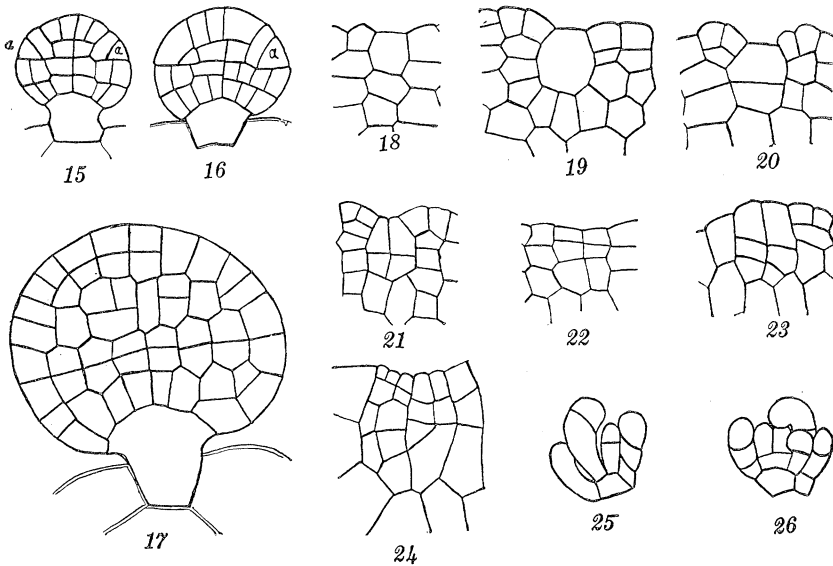
to the median wall before the apical cell becomes established. In case the two apical cells of a single gemma behave differently, there is an asymmetrical development of the gemma. If one apical cell becomes established before the other, it usually but not always ceases to function before the other; so that it is common to find a gemma with one apical cell cutting off a segment in the normal way while the other has already divided by a periclinal



FIGURES 5-14, *Radula flaccida*. Gemmae in various stages of development from single cell stage to the mature form. 5-7 show the gelatinous substance *m* and early divisions, $\times 400$. 8-12 show the apical cells *a*, $\times 400$. 14, mature gemma with funnellike elevation and basal cells, $\times 66$.

wall (FIG. 17). The same condition was observed in *R. complanata* by Stevens ('10, p. 370). This irregularity in the manner of establishment of the apical cell makes it possible to distinguish three types of gemmae: those in which the original apical quadrants begin immediately to function as apical cells (FIG. 9, 10, 11), those in which the apical quadrants cut off cells parallel with the

median wall before beginning to function as apical cells (FIG. 15), and those in which the establishment of the two apical cells is not simultaneous (FIG. 16). In any case the shape and size of the two sides of the gemma are not noticeably affected (FIG. 16 and 17). The two lower quadrants of the gemma mother cell do not produce apical cells but divide by longitudinal walls followed by transverse walls. After the apical cells in the upper half of the gemma cease to function, the whole gemma increases in size by the same method of cell division, followed by the inner or lower half from

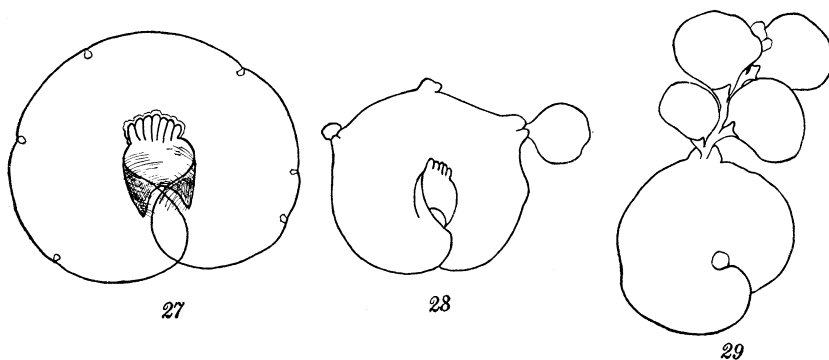


FIGURES 15-26, *Radula flaccida*. Gemmae with irregularities in the formation of the apical cells. 15, gemma which has cut off a segment on each side toward the median line before the apical cell has begun to function, $\times 400$. 16, gemma in which the development of the two apical cells is not simultaneous, $\times 400$. The apical cell on the left was formed from the original triangular quadrant, cut off one segment toward the median line, and ceased to function. The apical cell on the right was formed from the outer half of the original triangular quadrant and is still functioning. 17, gemma in which the apical cell on the left has ceased to function, while that on the right is still cutting off segments, $\times 533$. 18 and 19 show the method of the development of the marginal cell, which later produces the leafy shoot, $\times 400$. 20-22, stages in development of the leafy shoot from a single marginal cell, $\times 400$. 23 shows a variation in the sequence of cell division, $\times 400$. 24, dorsal view of later stage in development of the leafy shoot, $\times 533$. 25 and 26 show the leafy shoot, ventral view, developing in dextrorse and sinistrorse spirals, $\times 800$.

the beginning, each cell dividing by longitudinal walls followed by transverse walls; but as the gemma grows older the order of cell division is reversed, and the transverse walls are formed first and the longitudinal later.

In *R. Hedingeri* Goebel reports ('87, p. 52) that there are no apical cells whatever, and the gemma mother cell divides by a series of longitudinal walls between which transverse walls are formed.

Soon after the apical cells cease to function, the gemma begins to change its position and shape. Up to this time it has been a flat circular body protruding by the stalk cell beyond the margin of the leaf. Now the six or eight basal cells which attach the



FIGURES 27-29, *Radula flaccida*. 27, gemma at maturity, ventral view, showing the large marginal cells and the basal cells, $\times 66$. 28, germinating gemma showing one leafy shoot more advanced than the others, $\times 266$. 29, germinating gemma, later stage, with a well-developed leafy shoot, $\times 266$.

gemma to the stalk begin to grow, especially in length, and curve upwards so that they stand at right angles to the leaf. As this change in position takes place the cells adjacent to the large basal cells begin to divide and grow very rapidly, and to curve outward in such a way that the gemma again becomes parallel with the leaf surface but raised above it by a funnel-shaped tube. A short time before the gemma is mature several large cells become differentiated at intervals along the margin (FIG. 27). These vary in number from three to eight, but there are usually five. Each one arises through the enlargement of one of the peripheral cells, while the adjoining peripheral cells divide by periclinal walls

(FIG. 18 and 19). If the growth and division of the neighboring cells are very rapid, the large cell may appear in a temporary depression, but it soon increases in size so that the mature gemma shows no marginal indentations (FIG. 27).

After the large cells are fully differentiated, the gemma is shed. Shedding takes place by means of a splitting between the stalk cell and the long basal cells (FIG. 16). This splitting is probably caused by a gelatinization of the walls in this region. The stalk cell does not come off with the gemma, as it does in *R. complanata*, but remains a part of the leaf, as in the two species studied by Goebel ('87, f. 61). Cell divisions are now at an end until germination takes place, but the gemma may increase slightly in size by the enlargement of its individual cells. When mature it is a slightly concave disk with a funnellike outgrowth near the center and with the six large basal cells often adhering to the edge of the funnel.

All the germinating gemmae in this material were found on the lower surface of the leaves on which the plants were growing. It seemed remarkable that the spaces on the upper surface of the leaves were entirely free from isolated gemmae or young plants. After a gemma comes to rest with its concave side down, the first step in germination is the formation of rhizoids to anchor the young plant. These are developed from the cells near the periphery where the tissue comes in contact with the substratum. The rhizoids consist of short prolongations of the cells, with irregular lobes at the apex. According to Goebel ('87, p. 53, f. 66) the similar rhizoids in *R. Hedingeri* probably secrete a gelatinous substance by means of which they adhere to the substratum.

When the gemma is firmly anchored, the five large peripheral cells (FIG. 19) begin to divide (FIG. 20-23). The first wall is always periclinal, and the inner cell thus formed gives rise to the young shoot. The outer cell, as well as the neighboring cells, proceeds to divide and form a tissue which protrudes beyond the margin of the gemma (FIG. 20). This thalluslike body protects the tiny shoot coming out on the ventral side of the concave gemma. The sequence of divisions in the inner cell of the original peripheral cell is very complicated and difficult to follow; but a tetrahedral apical cell is soon formed, the divisions of which cor-

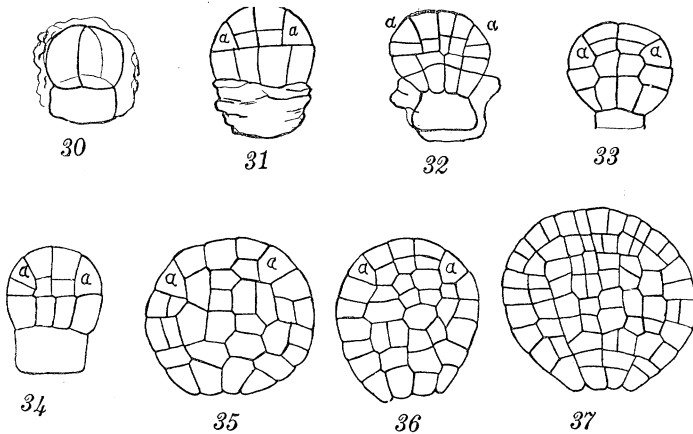
respond to those described by Leitgeb ('79) for the vegetative shoots of *R. complanata*, the cell cutting off segments on three sides only. The fourth face, which does not cut off segments, is the free one of the apical cell and lies toward the apex of the branch. Each segment cut off by a lateral face divides into two cells, an external cell and an internal cell. The external cell gives rise to the two lobes of the leaf and the cortical cells of the stem, while the internal cell by further division forms the axial cells of the stem. The segments cut off by the ventral face never form leaves but give rise to cells of the stem only. The three faces of the apical cell cut off their segments in spiral sequence, but the spiral may be either dextrorse or sinistrorse (FIG. 25 and 26).

RADULA PROTENSA

Lindenberg first described *R. protensa* from Java in 1848 (Meissner, p. 462). It is a tropical species native to Asia and various islands of the Pacific. The material used in this study was collected by Lamberto Loria in New Guinea (no. 114). *R. protensa* agrees with *R. flaccida* in being epiphyllous and prostrate. The gemmae are smaller than in *R. flaccida*, averaging only 0.2 mm. in diameter at time of shedding. It is possible, however, that the gemmae examined had not attained their full size, in spite of the fact that cell division had apparently ceased. In this species gemmae occur on vegetative branches and on male bracts. Schiffner ('93, p. 249) reports them also on the margins of old perianths. They are most commonly found scattered over the ventral surface of the leaves or along the margins and stand at right angles to the surface. They usually appear in groups, a single leaf sometimes bearing fifty or more in various stages of development.

As in *R. flaccida* the development of the gemma begins by the protrusion of an ordinary leaf cell. This cell, however, unlike that of *R. flaccida*, may occur in the surface of the leaf or in the margin. It also becomes covered with a much heavier covering of gelatinous material than is found in *R. flaccida*. The outer half of the cell is then cut off by a transverse wall. This division forms the stalk cell, which does not project beyond the surface of the leaf, and the gemma mother cell, which soon divides into

quadrants. The early walls are very delicate and scarcely show through the surrounding gelatinous layer. As the gemma increases in size it breaks through this sheath, which remains clinging to the base like a collar (FIG. 30). In the further development of the gemma the two apical quadrants function for a time as two-sided apical cells. As described for *R. flaccida*, the stage at which the apical cell becomes established and the stage at which it ceases to function vary. There is no curving or change in position in this gemma as is noted in *R. flaccida*; and at the time of shedding, the gemma is a circular body, one cell thick, slightly concave, but without any funnel-shaped outgrowth similar to that of *R. flaccida*.



FIGURES 30-37, *Radula protensa*. Stages in development of gemma from the two-celled stage until the apical cell ceases to function, $\times 400$. 30-32 show the stalk cell and the gelatinous sheath.

(FIG. 14). Shedding takes place by means of a splitting of the wall between the stalk cell and the basal cells. The stalk cell remains as a part of the leaf. The form of the gemma when shed is almost identical with that of the mature gemma of *R. Hedingeri*. Soon after shedding, the basal cells begin to elongate. On account of lack of germinating material it was impossible to trace the further development of the gemma. However, a few gemmae were found in which the marginal cells halfway between the basal cells and the apex, on one side or the other, were dividing and growing, apparently beginning to form a thalluslike outgrowth. So far as could be determined, there were no enlarged cells functioning as

differentiated peripheral growing points, and no gemmae were found in which the leafy shoot had begun to appear. Several young plants showed thalloid fragments clinging to them, but it was impossible to determine in any of these cases whether the fragment was a part of the gemma itself, as in *R. flaccida*, or part of a thallus such as is formed in *R. Hedingeri*.

RADULA LINDBERGIANA AND RADULA SUBTROPICA

R. Lindbergiana, a species native to Europe, Asia, and Algeria, first described by Gottsche in 1864, and *R. subtropica*, native to Brazil, and described by Stephani in 1910, were also studied. In these the gemmae were essentially the same as those of *R. complanata* as figured by Stevens ('10, p. 370).

COMPARISON OF SPECIES

Gemmae in the genus *Radula* may be arranged in two groups according to their complexity. The first group contains the simplest types and has representatives in three species, *R. complanata*, *R. Lindbergiana*, and *R. subtropica*. The gemmae in this group occur on the margins of leaves and are very irregular in size and shape when mature. This irregularity is due to the variation in the number and activity of the apical cells and their method of development. These gemmae may be more than one cell thick. Germination in this group has not yet been described. The second group contains the more complex types and has representatives in four species, *R. protensa*, *R. Hedingeri*, *R. tjibodensis*, and *R. flaccida*. These gemmae occur not only on the margins but also on the surface of leaves and follow a more regular course of development, the mature gemmae in a given species being uniform in shape and size. In *R. flaccida* and *R. protensa* apical cells are present, but *R. Hedingeri* and *R. tjibodensis*, while developing after a fixed plan, do not, according to Goebel ('87, p. 62), possess any apical cells. All the gemmae belonging to this group are only one cell thick. Germination in this group may be divided into two categories. In the gemmae of *R. Hedingeri*, and *R. tjibodensis*, as described by Goebel, the procedure is as follows: The circular gemma develops at some point on the margin a thalluslike body as large as the gemma itself. One of the marginal cells of this thalloid outgrowth in turn gives rise to the leafy shoot, but by the continued growth of the tissue adjoining

this marginal cell the shoot later appears to arise from the central part of the thallus. The second type of procedure is seen in the germinating gemmae of *R. flaccida*. In this species from five to eight differentiated peripheral growing points immediately give rise to the apical cell of the shoot. The formation of a thallus-like body preliminary to this stage seems to be suppressed. The growth of the outer peripheral cell and its adjoining cells in *R. flaccida* to form a thallus, corresponds to the growth of the thallus in *R. Hedingeri* after the differentiation of the apical cell of the shoot. *R. protensa* probably belongs to the first category and germinates according to the procedure followed by *R. Hedingeri*.

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